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DISTRIBUTION AND LIFE HISTORY OF *EUPHAUSIA TRIACANTHA* HOLT AND TATTERSALL

by

A. de C. Baker

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By

A. de C. BAKER

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THE DISTRIBUTION AND LIFE HISTORY OF *EUPHAUSIA TRIACANTHA* HOLT AND TATTERSALL

By A. de C. Baker

(Text-figs. 1–16)

INTRODUCTION

One approach to the problem of revealing the basic principles governing the distribution of planktonic organisms is to make special studies of selected representative species. Detailed examination and comparison of species with different distributional, reproductive and feeding habits should help to elucidate the factors controlling these habits.

David (1955) has already made such a study of the carnivore, *Sagitta gazellae* Ritter-Zahony, 1909, from the Discovery collections and Mr J. W. S. Marr, who is working on *Euphausia superba* Dana, 1852, has published a preliminary account of the broad features of its distribution (1956). The present paper on *E. triacantha* Holt and Tattersall, 1906, is intended as a further contribution to this work.

There are several reasons for selecting *E. triacantha* as a species for detailed examination. John (1936) has shown that the distribution of the southern members of the genus *Euphausia* is such that they occur in more or less overlapping concentric zones round the Antarctic continent. *E. superba* occurs in the East Wind drift and Weddell Sea regions of the Southern Ocean (Marr, 1956) and *E. triacantha* is found to the north of this in the West Wind drift (John, 1936); thus a useful comparison can be drawn between the two species. Also *E. triacantha* displays little or none of the shoaling habit found in *E. superba*. That *E. triacantha* performs a marked diurnal vertical migration, a character not found in *Sagitta gazellae* (David, 1955) nor in *E. superba* (Mr Marr, personal communication), is of additional interest for purposes of comparison. It is also easily identified in the samples, a point of some considerable importance where much material has to be examined.

ACKNOWLEDGEMENTS

This study was undertaken at the suggestion of Dr N. A. Mackintosh, C.B.E., who has given me much helpful advice and criticism.

I would also like to express my thanks to those of my colleagues who have given me help and advice from time to time, particularly to Mr J. W. S. Marr for allowing me to use his data for the section concerning *E. superba* and also for reading and criticizing the draft of that section; to Dr H. E. Bargmann for her assistance during the study of the reproductive system; to Mr P. M. David for reading and criticizing the typescript and to Mr P. Foxton for allowing me to make use of the data he collected during the sixth Antarctic commission (1950–1) of R.R.S. 'Discovery II'.

I would also like to thank Mr A. E. Fisher who helped me in the early stages of this work by sorting many samples, and Mr A. Style who prepared several of the figures for publication.

PREVIOUS WORK ON THE SPECIES

Since the original description by Holt and Tattersall (1906), based on a single male specimen taken by the National Antarctic Expedition, *E. triacantha* has been described from the material taken by many of the major expeditions to the Southern Ocean. In 1902 the Swedish Antarctic Expedition took this species at four stations in the eastern south Atlantic. At one station in June Hansen (1913, p. 34) records 'numerous specimens' and also that the stages of development at another station in April ranged 'from very young to full grown'. Hansen gives a fuller description than was possible from the type specimen and includes an account of the copulatory organs. Zimmer (1914) records five specimens taken by the Deutsche Sudpolar-Expedition in the Indian Ocean, and Illig (1930) records four specimens taken by the Deutsche Tiefsee-Expedition. Tattersall (1924), in a survey of the Subantarctic and Antarctic euphausiids, considered that *E. triacantha* was entirely a Subantarctic species. The 'Norvegia' Expedition 1927–8 and 1928–9 took six specimens, five females and one larva. This larva, a second furcilia, was the first that had been taken and Rustad (1930) describes it in some detail. The later 'Norvegia' Expeditions, 1929–30 and 1930–1, took fewer adults but provided material for the description of the first, second and third calyptopes (Rustad, 1934). Ruud (1932), in an account of the Euphausiidae taken on the whaling expedition of S.S. 'Vikingen' in 1929–30, mentions fifteen specimens that were taken, and suggests that the species belongs to the warm deep water. He also describes two metanauplii which he believes 'very probably belong to one of the two species, *E. frigida* or *E. triacantha*'.

Subsequent work has mainly been based upon material from the 'Discovery' collections. Mackintosh (1934), in his account of the distribution of the macroplankton in the neighbourhood of the Falkland Island Dependencies, includes *E. triacantha* in the species which probably belong only to the Antarctic water but which occasionally stray into Subantarctic water. He also points out that the numbers taken in the surface show a marked diurnal variation. This diurnal variation was also observed by Hardy and Gunther (1935) who note the almost complete absence of the species from the upper 200 m. during daylight hours and conclude that this is due to a diurnal vertical migration. They also note that at times it was 'moderately abundant' off the north and north-eastern coast of South Georgia and that it was present at only one station in the region to the south and south-west of the island.

In his account of the southern species of the genus *Euphausia* John (1936) gives a full description of the adults and of the larvae from the second calyptopis upwards. He distinguishes seven furcilia stages and gives length ranges for these and the calyptopis stages. From the examination of the characteristics, mainly of the copulatory organs, of Hansens Group *d* (1911), he shows this to be a natural group and suggests that the four species, *E. hanseni* Zimmer, 1915, *E. spinifera* Sars, 1885, *E. longirostris* Hansen, 1908 and *E. triacantha*, represent stages in the colonization of the cold southern water, *E. hanseni* being the most northern and *E. triacantha* the most southern species of the group. Regarding the distribution he shows that *E. triacantha* occurs to the north of the northern limit of the pack-ice and in a narrow belt of the Subantarctic. He also suggests that breeding takes place in this narrower, Subantarctic, part of its range.

While considering the vertical distribution of the Antarctic macroplankton Mackintosh (1937) suggests that, in spite of the rather scanty material taken by the 70 cm. vertical nets, *E. triacantha* can be included among those species that perform an energetic daily migration but no extensive annual migration. He also points out that the limits of distribution of a species may be controlled by migration between the northward moving surface water and the southward moving deep water.

Other descriptions and references to the distribution of *E. triacantha* are included in Tattersall (1908, 1913) and Hansen (1911); keys are to be found in Tattersall (1925), Rustad (1930) and Sheard (1953).

MATERIAL AND METHODS

This paper is based upon material contained in the plankton samples of the Discovery Collections. The samples used were largely those collected by means of oblique hauls with the 100 cm. diameter net (N 100 B) but, for the purpose of studying vertical distribution, samples obtained from vertical hauls with the 70 cm. closing net (N 70 V) have also been used and a number of samples from oblique hauls with the young fish trawl (TYFB) have been examined where it was necessary to fill in gaps in the distribution chart.

The N 100 B was fished for 20 min. from approximately 100 m. to the surface and, at some stations, also from 250 to 100 m. and 500 to 250 m. During these deeper hauls the net was closed at the upper horizon before being brought to the surface. At the majority of stations the N 70 V was fished at six depths: 50–0, 100–50, 250–100, 500–250, 750–500, and 1000–750 m.; an additional haul from 1500–1000 m. was also fished at a good many stations. Details of the construction and the methods employed in working these nets can be found in Kemp, Hardy and Mackintosh (1929).

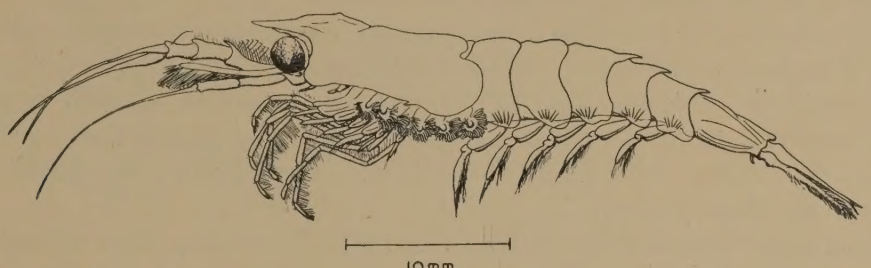

Fig. 1. Adult female *E. triacantha*.

By no means all the available material has been used for this study. The samples have been chosen largely from certain lines or groups of stations in order to give adequate coverage of the Southern Ocean at different times of year and to represent the principal features of the distribution of the species. It is very unlikely that the method of selection has introduced any accidental bias which affects the results. A great many samples had already been analysed by other workers for different purposes before this present work was started, and these analyses, which consist of counts, or both counts and measurements, have been used where possible.

Where a large number of samples have to be examined the time involved depends to a great extent on the ease with which the species can be identified. Adult *E. triacantha* can usually be picked out quite readily on its general appearance alone, but in cases of doubt it can be distinguished from the other related species with mid-dorsal spines on the third to fifth abdominal segments, i.e. *E. hanseni*, *E. spinifera* and *E. longirostris*, by the absence of post-ocular spines (Fig. 1). The larvae are also fairly easily identified, either by the strong median spine on the posterior margin of the carapace in the first calyptopis to first furcilia, or by the presence, in the later stages, of the mid-dorsal abdominal spines. They can be distinguished from the larvae of *E. spinifera* and *E. longirostris* in all these stages by the absence of denticles on the margin of the frontal plate.

The lengths given in this paper have been measured from the anterior margin of the eyes to the tip of the telson.

Except for those specimens collected during the earlier years of the Discovery Investigations, when crustacea picked out of samples were preserved in alcohol, all the material is preserved in neutralized sea-water formalin.

HORIZONTAL DISTRIBUTION OF ADOLESCENTS AND ADULTS

Range in Antarctic and Subantarctic water

In the preparation of the chart (Fig. 2) and other figures showing the horizontal distribution of adolescent and adult *E. triacantha* the data used have been limited to oblique hauls made at night between approximately 100 m. and the surface with the 100 cm. diameter net. There are two reasons for this limitation of the data. First, although the N70V hauls provide valuable information on the vertical distribution of larval stages, the numbers of adolescents and adults taken in these nets are small where a comparison of the populations of different regions is required. Secondly, as mentioned above, *E. triacantha* performs a marked diurnal vertical migration and consequently hauls are strictly comparable only when taken through the same depth range at the same hour of the day or night. In selecting the stations for plotting in Fig. 2 it was considered sufficient if they had been worked during the hours of darkness. However, owing to the routine adopted for station work, over 75% of the hauls were, in fact, taken between 2100 and 0100 hrs.

In Fig. 2 the number of *E. triacantha* at each station is shown according to the scale on the chart. North of 50° S between 30° W and 60° W no N100B hauls are available. In this area, therefore, oblique hauls with the young fish trawl (TYF) have been examined, but only to determine the presence or absence of *E. triacantha*, since the quantities sampled by this larger net are not comparable with those from the 1 m. net. Presence at these stations is indicated by a cross. Absence is shown by an open circle in the usual manner.

The Southern Ocean consists of a continuous circumpolar belt of deep water in which the environment is more or less uniform from east to west and in which changes take place from north to south. Broadly speaking this results in the distribution of the planktonic species in circumpolar belts of greater or lesser width. It has been shown (Baker, 1954) that within these belts there is no longitude in which the commoner macroplankton species, including *E. triacantha*, may not be found (Fig. 2).

While considering the distribution of *E. triacantha*, John (1936, p. 232) states that 'it occurs throughout the ice-free water of the Antarctic Zone'. The present more detailed study shows this to be true, as will be seen from the distribution chart. However, there is a very marked concentration in the region of the Antarctic convergence, and where it has been taken in the higher latitudes the catches tend to be small. It also occurs consistently to the north of the Antarctic convergence and this southern zone of the Subantarctic water must be considered as part of the normal habitat.

Except possibly in the south-western Atlantic, *E. triacantha* shows a close association with the Antarctic convergence throughout its circumpolar range. Because of this association the latitudinal distribution in relation to the convergence can be examined by using it as a datum line.

In Fig. 3, six meridional lines of stations are plotted according to the distance of the stations north or south of the Antarctic convergence. The positions of the convergence shown in the figure are from observations made at the time of crossing, and have been taken from Mackintosh (1946, Table 9). The number of animals taken at each station is shown as a percentage of the total number of animals taken along each line of stations. The lines have been selected so that different longitudes and months are represented. It will be seen from this diagram that, although the total range of *E. triacantha* may extend from 450 miles to the north of the convergence to 650 miles to the south, in all these lines of stations at least 60% of the population in the surface waters at night occurs in the region 150 miles north to 200 miles south of the convergence.

It is generally accepted that the Antarctic convergence can act as an important faunistic boundary (Mackintosh, 1934, p. 83; Ommaney, 1936, pp. 298–9). David (1955) found that, although the

Fig. 2. The horizontal distribution of adolescent and adult *E. triacantha* in the upper 100 m. of water at night based upon shallow oblique hauls with the 1 m. net. The mean position of the Antarctic convergence and the mean northern limit of the pack-ice are shown.

chaetognath *Sagitta gazellae* was present in both Antarctic and Subantarctic waters the catches were extremely small in a region 100 miles north to 200 miles south of the convergence and he distinguished separate races in the population to the north and south of it. It will be clear from Fig. 3 that the pattern of distribution for *E. triacantha* is the reverse of that for *S. gazellae* and that the catches in fact reach a maximum in the vicinity of the convergence. David suggests that it is likely that the sudden changes in physical conditions, brought about by the fluctuations in the position of the Antarctic convergence, are unfavourable to *S. gazellae*. In the case of *E. triacantha*, however, such conditions are evidently favourable.

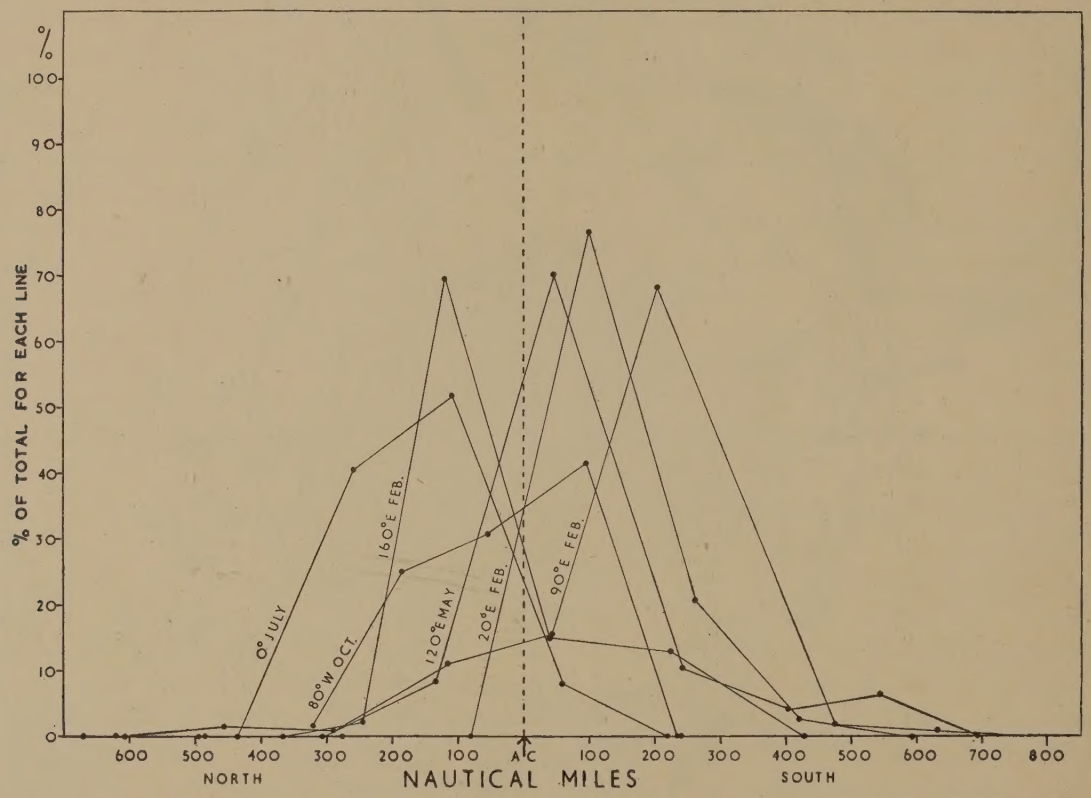

Fig. 3. The number of adolescent and adult *E. triacantha* in a series of shallow oblique night hauls with the 1 m. net from north-south lines of stations plotted according to the distance in nautical miles from the Antarctic convergence. The number per 20 min. haul is expressed as a percentage of the total catch for each line. The position of the convergence has been taken from Mackintosh (1946, Table 9).

Seasonal variation

In Fig. 4 the distribution of adolescent and adult *E. triacantha* in relation to the Antarctic convergence is shown for each season of the year. The mean catch per 20 min. haul has been plotted at intervals of 50 miles north and south of the convergence. The crosses indicate the intervals for which no data are available. In order to obtain sufficient observations lines of stations from several different regions of the Southern Ocean have been used; the number taken from each sector in each season is shown in Table 1. The exact position of the convergence was indeterminate for a line of stations (2311–2320) along the Greenwich meridian in April and the mean position of 49° 50′ S, based on nine other lines along the same meridian, has been used as an approximation. This is unlikely to fall more than 20 miles from the actual position and as the observations are in 50-mile groups no significant error

is involved. The year has been divided into seasons as follows: summer, December–February; autumn, March–May; winter, June–August; spring, September–November.

It will be seen from Fig. 4 that, except for the large number taken between 300 and 350 miles north of the convergence in summer, the region of maximum abundance, at least in the upper 100 m., bears very much the same relationship to the convergence throughout the year. The number of observations in each 50-mile interval varies considerably and where these are very low the value

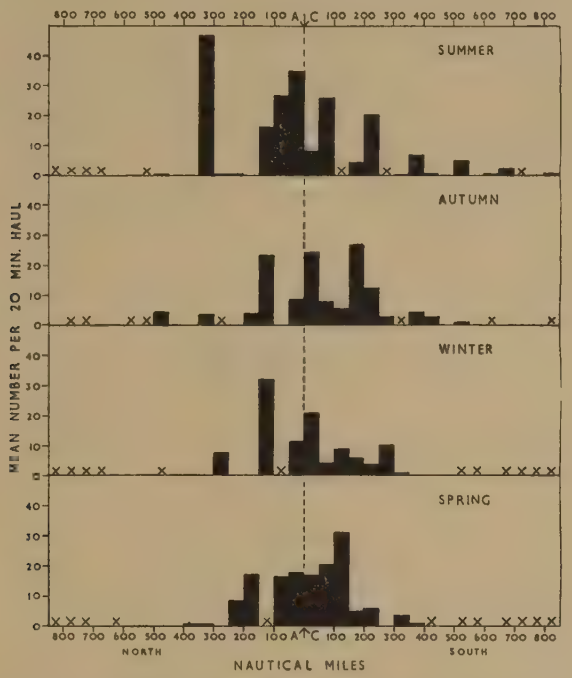

Fig. 4. The seasonal variation in horizontal distribution of adolescent and adult *E. triacantha* in relation to the Antarctic convergence. The mean number of specimens per 20 min. haul has been calculated for each 50-mile belt north and south of the convergence. Belts in which no observations are available are indicated by crosses.

Table 1. *The lines of stations used for Fig. 4, showing the sectors in which they were worked. The figures in brackets indicate the number of stations used in each line*

	Season			
Sector	*Summer*	*Autumn*	*Winter*	*Spring*
0°–90° E	2492–2500 (5)	1361–1369 (9)	1788–1801 (9)	1806–1813 (6)
	2531–2541 (6)	1772–1781 (8)	2355–2362 (7)	2425–2430 (4)
	2565–2576 (8)	2311–2320 (5)	2378–2380 (3)	2446–2453 (6)
	2582–2592 (8)	2340–2350 (5)	2385–2393 (4)	2459–2465 (5)
	—	2612–2625 (9)	2411–2419 (6)	—
90° E–180°	1675–1682 (6)	879– 887 (9)	898– 906 (7)	—
	2155–2168 (9)	1723–1733 (6)	913– 923 (8)	—
	2204–2212 (5)	—	—	—
	2802–2811 (9)	—	—	—
180°–90° W	—	—	—	946– 951 (6)
	—	—	—	2736–2745 (8)
90° W–0°	1222–1228 (4)	1312–1320 (5)	—	1027–1035 (5)
	—	—	—	1415–1421 (4)
	—	—	—	1442–1450 (5)

obtained for the mean number per 20 min. haul gives only a very approximate indication of the level of abundance. This applies particularly to the high figure 300 miles north of the convergence in summer which is based on only one observation, St. 1228, in December, at which a large catch of post larval specimens were taken.

The diagram shows the spread to the south as being greater in summer than during the rest of the year. This is due to the inclusion of four lines of stations worked in the 90° E–180° region where, as will be shown below, the total range is considerably greater than in other sectors.

Regional variation

In Fig. 5 mean numbers per 20 min. haul from a series of observations made along the Greenwich meridian are compared with those from a similar series made between 90° E and 170° E. The data have been treated in the same manner as in Fig. 4.

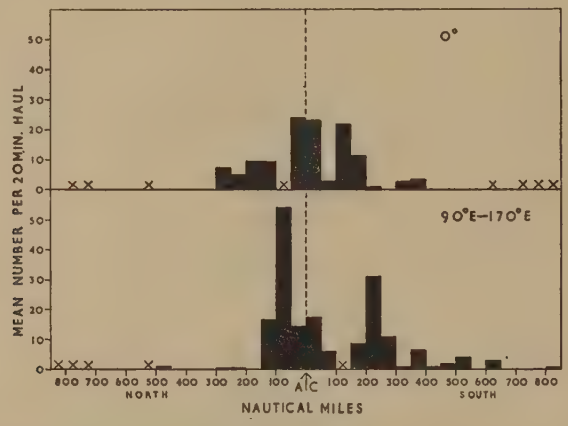

Fig. 5. The distribution of adolescent and adult *E. triacantha* in relation to the Antarctic convergence in the Greenwich meridian compared with that in the sector 90° E–170° E (see Fig. 4 for explanation).

It will be seen that the total north–south range is considerably greater between 90° E and 170° E than on the 0° line; it extends over 1350 miles in the former and only 700 miles in the latter. The range over which *E. triacantha* is abundant is, however, similar in both regions, though in the Greenwich meridian the northern and southern limits are some 150–200 miles further north.

There is little doubt that the southward spread of *E. triacantha* in the South Atlantic (0°) is restricted, at least to some extent, by the Weddell drift, the core of which crosses the Greenwich meridian in about 60° S (Deacon, 1937, p. 28). The northern limit of the Weddell drift is not clearly defined, but Deacon (p. 25) records two occasions in the mid-South Atlantic when a marked temperature change has indicated a convergence between Antarctic water coming from the north of Graham Land through Drake Passage and that from the Weddell Sea. One occurred in approximately 55° S, 22° W and the other, less clearly marked, between 51° 20′ S, 07° E and 52° S, 06° E. The boundary, being further south to the west of these last two positions, is likely, in 0°, to occur between 53° S and 54° S. This corresponds to a position some 130–250 miles south of the mean position of the Antarctic convergence in 0° and it will be seen from Fig. 5 that the number of *E. triacantha* fall off considerably in this region. Ommaney (1936, p. 297) found a similar distribution in *Rhincalanus gigas* Brady, 1883, that is a falling off in numbers to a level of comparative scarcity in the Weddell Sea water.

In the Indian Ocean (Fig. 5, 90° E–170° E), although the numbers are small beyond 400 miles south of the Antarctic convergence, the total range extends as far south as the boundary between the East and West Wind drifts.

Distribution in relation to surface temperature

The extreme range of surface temperature over which *E. triacantha* has been found is −1·80° C. (St. 463) to 11·88° C. (St. 2803); two specimens only were taken at each of these stations. The 100–0 m. N 100 B night hauls have been grouped according to the season and the surface temperature, using 2° C. intervals, and the mean catch per 20 min. haul calculated for each group. These means are shown in Table 2. At two stations, 2807 in summer and 452 in spring, unusually large catches have raised the mean considerably and the values obtained when these catches are omitted are shown in brackets. It can be seen that, except during the spring, the greater part of the population lives in a zone in which the surface temperatures are between 2 and 8° C.

E. triacantha is an inhabitant of the West Wind drift and is virtually excluded from the Weddell Sea water and the East Wind drift. It is clear from the surface temperature range mentioned above and from the moderately large catches taken in the West Wind drift in spring that the exclusion from the Weddell Sea and East Wind drift cannot only be due to an intolerance of low surface temperatures.

Table 2. *Seasonal variation with surface temperature of the mean number of adolescent and adult* Euphausia triacantha *per 20 min. haul. Means calculated for 2° C intervals (see text for explanation of figures in brackets)*

Surface temperature (° C.)	*Summer*		*Autumn*		*Winter*		*Spring*	
	Mean	*No. obs.*	*Mean*	*No. obs.*	*Mean*	*No. obs.*	*Mean*	*No. obs.*
−2·00–−0·01	0·74	19	1·13	16	4·40	35	7·30	69
0·00–1·99	1·61	36	6·20	46	10·68	18	13·09 (9·22)	33
2·00–3·99	9·70 (7·58)	37	14·08	36	12·36	11	11·37	19
4·00–5·99	16·69	16	10·88	17	15·70	10	5·21	24
6·00–7·99	19·11	9	4·07	15	3·00	8	0·36	11
8·00–9·99	0·25	8	0·67	6	0·00	7	0·00	8
10·00–11·99	0·43	7	0·00	4	0·00	4	0·00	1
12·00–13·99	0·00	1	0·00	3	0·00	3	0·00	4

Referring back to Fig. 2 (circumpolar chart) it will be seen that in the east and mid-south Atlantic the southern limit of distribution corresponds very closely with the mean northern position of the pack-ice, and it is possible that the pack-ice has some influence on the southward spread of the species. That this correlation does not occur to the same extent in the Pacific and Indian Oceans suggests that the pack-ice is not the sole limiting factor.

It is possible, in a species such as *E. triacantha* which performs an extensive diurnal migration, that the temperature at the lower level of the vertical range may have a controlling influence on the horizontal distribution. It has been found that the southern limit of distribution of *E. triacantha* falls close to the position of the 1° C. isotherm at 600 m. but it is impossible at present to examine this correlation more closely.

Moore (1952) has suggested that the limits of distribution, both horizontal and vertical, of diurnally migrating euphausiid species may be controlled by a balance between temperature and illumination, but to study this balance in the case of *E. triacantha* a great deal of information would be required on the illumination at different depths in the Antarctic.

Euphausia triacantha and *E. superba*

In Fig. 6 the distribution of adolescent and adult *E. triacantha* is plotted with that of *E. superba* over 20 mm. long. The data are derived from both day and night hauls from 100 m. to the surface with the N 100 B. Mr J. W. S. Marr has kindly allowed me to use his unpublished data on *E. superba* for

this figure. (The data from horizontal surface hauls with the 1 m. net (N 100 H) have been published in Marr, 1956, Fig. 1.) The sizes of the symbols used in Fig. 6 to indicate the numbers per 20 min. haul are the same for both species; for the sake of clarity negative stations have been omitted.

The figure shows the great difference between the numbers of *E. triacantha* and those of *E. superba*;

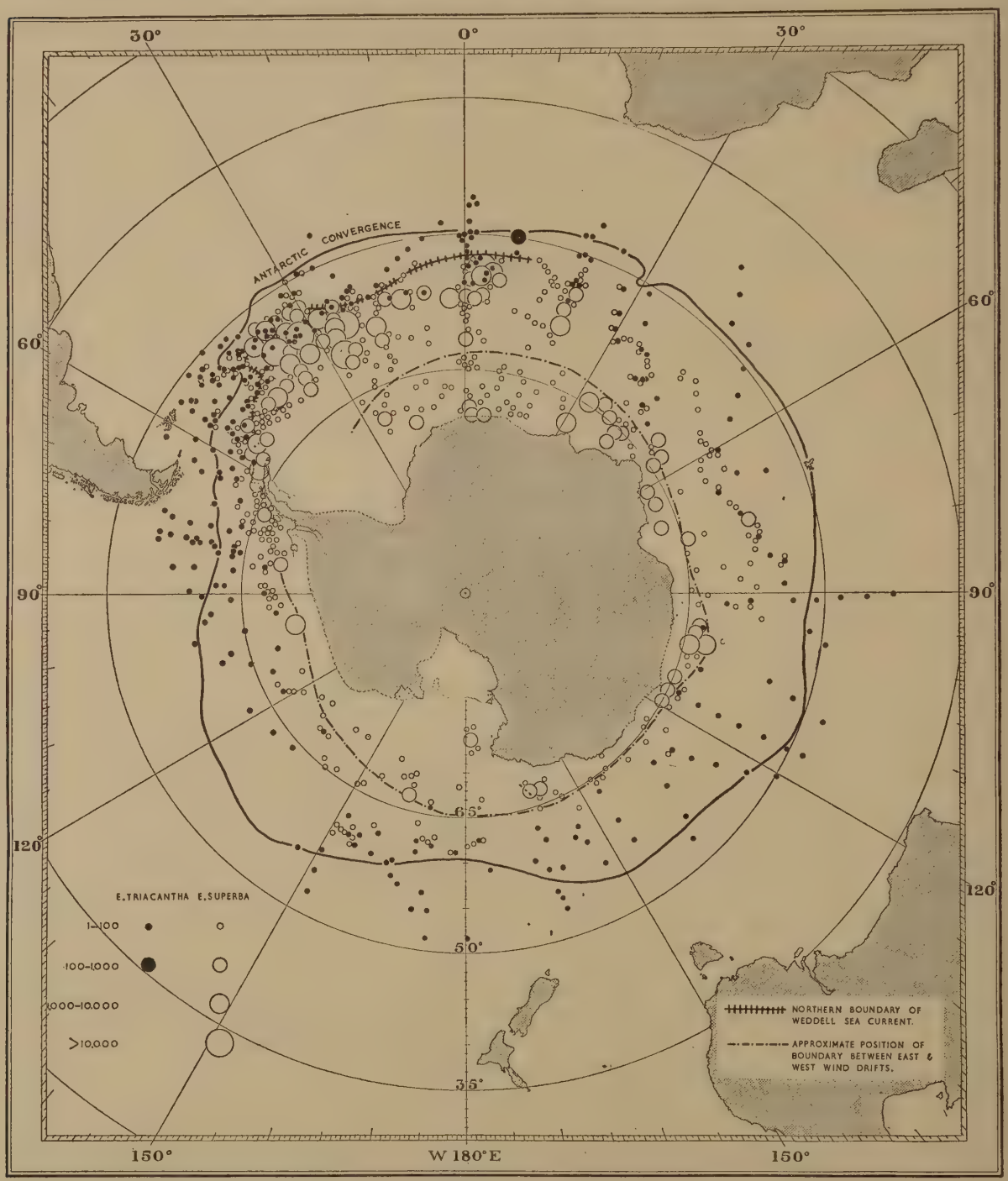

Fig. 6. The horizontal distribution of adolescent and adult *E. triacantha* taken in shallow oblique hauls with the 1 m. net during the day and night compared with the distribution of *E. superba* over 20 mm. long from similar hauls.

except at one station (St. 452) *E. triacantha* has not exceeded 100 per 20 min. haul, whereas *E. superba*, even when only those over 20 mm. are considered, exceeded 10,000 at four stations. It also shows that, although mixing of these species does occur, in general they are confined to different water masses, *E. triacantha* to the West-Wind drift and *E. superba* to the East Wind and Weddell drifts. The mixing is only found at the junction of these water masses and is most marked in the region of South Georgia where, as pointed out by Hardy and Gunther (1935), hydrological conditions are complex.

HORIZONTAL DISTRIBUTION OF LARVAE

The larvae considered here include the first, second and third calyptopis stages and the seven furcilia stages described by John (1936, p. 278). The data presented in Fig. 7 are based upon night hauls

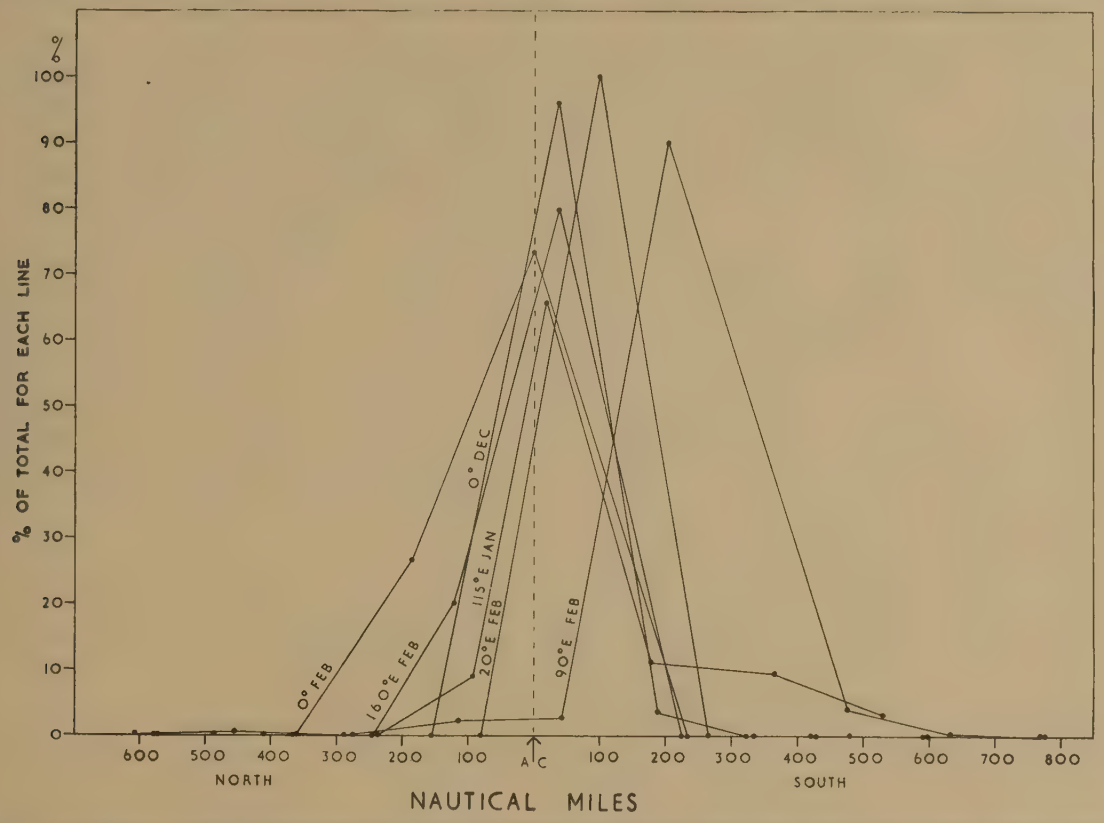

Fig. 7. The number of larval *E. triacantha* in a series of shallow oblique night hauls with the 1 m. net from north-south lines of stations plotted according to the distance in nautical miles from the Antarctic convergence. The number per haul is expressed as a percentage of the total catch for each line. The position of the convergence has been taken from Mackintosh (1946, Table 9).

between 100 m. and the surface with N 100 B and it is possible that the mesh of this net is not small enough to take representative samples of the first and second calyptopis stages. However, the meridional lines of stations used in preparing this figure were worked in December, January and February, during which months the predominant larval stages, as will be shown later (p. 334), are the second to seventh furcilias. The data for the larvae have been treated in the same manner as those for the adolescents and adults, that is, the number of larvae taken at each station is shown as a percentage of the total number of larvae taken along each line.

The total north to south range of the larvae, as shown in this figure, is approximately the same as

that of the adults but, in general, the region of abundance is a belt extending for 200 miles south of the Antarctic convergence. This, however, is not always so; in the Falkland sector the region of abundance extends for about 200 miles to the north of the convergence and at Station 1880 (Fig. 8) in 45° 53·8′ S, some 650 miles north of the mean position of the convergence, moderately large numbers (93) of third calyptopes and first, second and third furcilias were taken in an N 100 B. This station, at which the temperature was 7·47° C. at the surface and 3·95° C. at 100 m. lies in the path

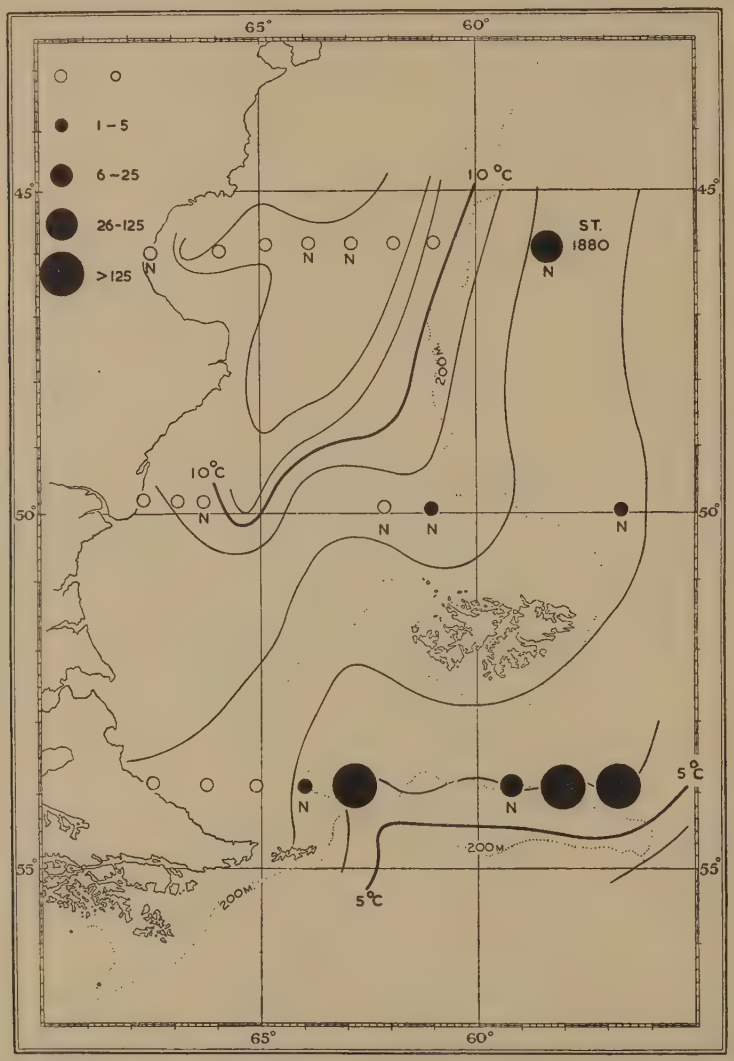

Fig. 8. The distribution of larval *E. triacantha* on the Patagonian shelf and slope from shallow oblique hauls with the 1 m. net. Night stations marked N. Isotherms taken from an unpublished internal report.

of the relatively cold Falkland current which runs northwards from Cape Horn and extends over the Patagonian continental shelf and slope (Deacon, 1937, p. 51). As shown in Fig. 8 a concentration of larvae was found in the Subantarctic water east of Cape Horn and some of these were probably carried north in this current.

Fig. 8 shows three east–west lines of stations which started in oceanic water and ran in towards the Patagonian coast over the slope and shelf. These have been used to determine whether or not *E. triacantha* larvae are present in shelf water. Many of these stations were worked during daylight

hours when the 100–0 m. N 100 B would not normally be expected to take a representative sample of the species owing to its diurnal vertical movements. However, at several day stations on the shelf nearly the whole water column was sampled, the net fishing to within 20 m. of the bottom, so unless the larvae were lying either on or very close to the bottom, for which there is no evidence one way or the other, these stations can be used as evidence of the presence or absence of *E. triacantha*. Night stations are indicated in the figure by the letter N.

It can be seen that, although moderately large catches of larvae were taken off the edge of the shelf even in daylight, they were only taken at two stations inside the 200 m. contour and there was only one larva at each of these.

VERTICAL DISTRIBUTION OF ADOLESCENTS AND ADULTS

In considering the vertical distribution of *E. triacantha* it is necessary to take into account the diurnal vertical migration, the existence of which was shown by Mackintosh (1934, 1937) and Hardy and Gunther (1935). Mackintosh, while studying the effect of diurnal variations upon the catches in the

Table 3. *Diurnal variation in the numbers of adolescent and adult* Euphausia triacantha *taken at stations within its normal horizontal range by the* 100–0 *m. N* 100 *B*

	Total no. of hauls	*No. of positive hauls*	*% of positive hauls*	*Total no. of* E. triacantha	*Mean no.* E. triacantha *per haul. All hauls*	*Mean no.* E. triacantha *per haul. Positive hauls only*
Day	379	6	1·6	17	0·045	2·8
Night	430	292	67·9	4016	9·340	13·8

100–0 m. N 100 B, found that *E. triacantha* was taken in only three out of 127 hauls made between 0600 and 1759 hrs. This diurnal variation in the numbers in the upper 100 m. is confirmed and shown to be even more marked by the present data. It will be seen from Table 3 that of 379 hauls taken during daylight hours within the horizontal range of adolescent and adult *E. triacantha* (see Table 4)

Table 4. *The approximate northern and southern limits of* Euphausia triacantha *in each* 10° *of longitude. Only stations falling within these limits have been used in assessing diurnal migration*

	East longitude		*West longitude*	
Sector	*Northern limit* (° S)	*Southern limit* (° S)	*Northern limit* (° S)	*Southern limit* (° S)
0°–10°	46	54	47	54
10°–20°	47	54	48·5	54·5
20°–30°	47	54·5	46	54·5
30°–40°	47	57	50	55·5
40°–50°	47	57	50	58·5
50°–60°	47	55·5	50	60
60°–70°	50	58	55	61
70°–80°	51	58	55	65
80°–90°	51	58	55	69
90°–100°	49	60	58	69
100°–110°	49	60	58	65
110°–120°	49	60	58	65
120°–130°	50·5	60	58	65
130°–140°	52	60	58	65
140°–150°	52	60	56	65
150°–160°	54	60	56	62·5
160°–170°	54	62	56	62·5
170°–180°	57	64	53·5	62·5

it was present in only 1·6%, whereas it was present in 67·9% of similar hauls taken during the night. It is also clear from Table 3 that on the few occasions it has been taken in the upper 100 m. during the day it has only been present in small numbers, the mean number per haul, considering positive hauls, only being 2·8; the corresponding figure for night hauls is 13·8.

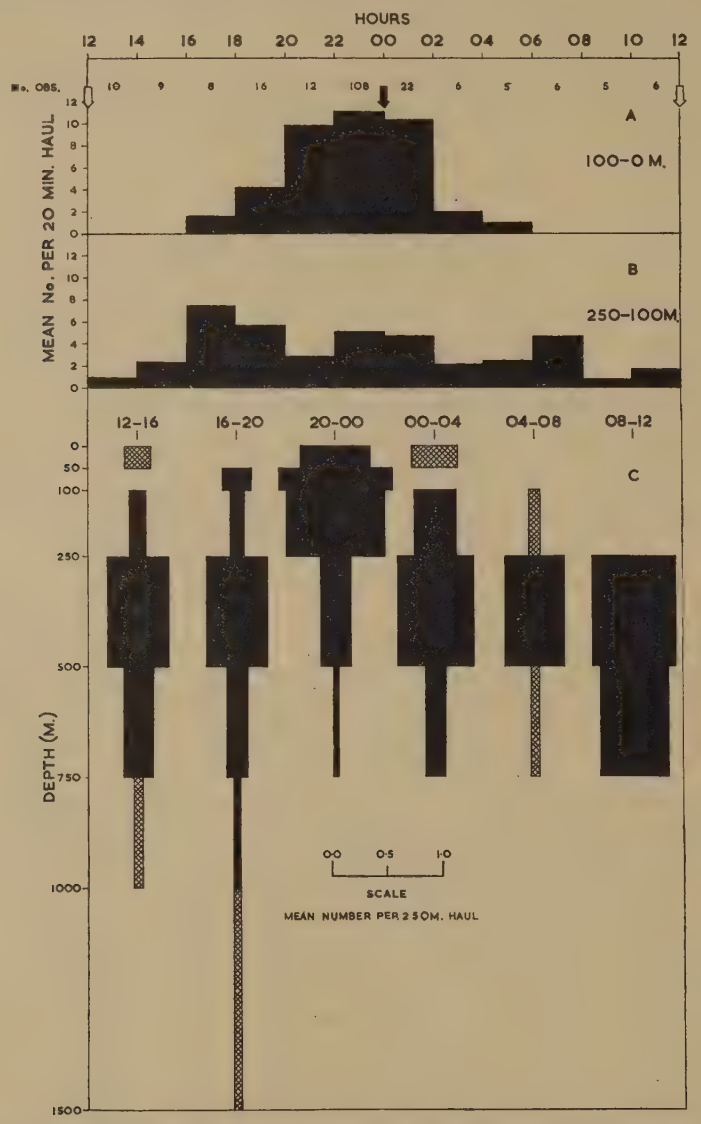

Fig. 9. The daily vertical distribution of adolescent and adult *E. triacantha*. A, the mean number per 20 min. N 100 B haul in the upper 100 m. for each 2-hourly period. B, the mean number per 20 min. N 100 B haul between 250–100 m. for each 2-hourly period. C, the mean number per 250 m. N 70 V haul for each 4-hourly period. Cross-hatching indicates means based on only one specimen. (See Table 5 for the number of observations on which this figure is based.)

The diurnal variation in the numbers in the surface water could be caused by a diurnal variation in avoidance of the net. However, it is shown below (p. 328) that there is no such difference between day and night avoidance, and consequently this must be a real variation in the population and not just an apparent one due to the sampling methods.

Fig. 9 A and B shows the mean number of adolescent and adult *E. triacantha* per 20 min. 100–0 m. and 250–100 m. hauls, respectively, for each 2-hourly period. Only those stations have been used at

which simultaneous observations were made through each depth horizon. The 250–100 m. haul takes 30 min. and the numbers taken in these nets have been corrected for a 20 min. haul for comparison with the upper net. Although the two layers sampled are usually approximately 100–0 m. and 250–100 m., in some instances the upper net fished from 150–0 m. and the lower net started fishing as deep as 500 m.; no allowance has been made for this variation. The number of observations in each 2-hourly period varies greatly owing to the routine adopted for working stations.

It will be seen that between 0600 and 1600 hrs. adolescent and adult *E. triacantha* are absent from the upper 100 m. From 1600 to 2000 hrs. the numbers increase rather slowly, between 2000 and 2200 hrs. there is a more rapid increase and the maximum is reached between 2200 and midnight. The descent in the early morning follows a similar by slightly steeper curve. The pattern of distribution in the 250–100 m. layer is not so clear. Between 0800 and 1600 hrs. the numbers are low and the major part of the population must be below 250 m. Between 1600 and 0800 hrs. there is a considerable variation but there are two slight peaks between 1600 and 1800 hrs. and 0600 and 0800 hrs. and these probably represent part of the population passing through the layer during their ascent and descent. It is clear from this diagram that part of the population migrates upwards from a depth below 250 m. but does not continue up into the 100–0 m. layer.

Table 5. *The number of observations in each 4-hourly period and at each depth used in preparing Fig. 9C.*

	Time (hr.)					
Depth (m.)	*12–16*	*16–20*	*20–00*	*00–04*	*04–08*	*08–12*
50–0	21	37	149	12	13	39
100–50	21	37	149	13	13	39
250–100	21	36	149	12	14	38
500–250	18	36	148	13	13	38
750–500	15	36	140	11	13	37
1000–750	13	34	134	7	13	36
1500–1000	1	7	43	0	0	2

There are not enough samples from 1 m. nets hauled below 250 m. to give helpful data, and, as has been stated above, the vertical hauls with the 70 cm. diameter net do not provide adequate data concerning the distribution of adult euphausiids of the size and comparative scarceness of *E. triacantha*. In spite of this it was felt that some measure of the population below 250 m. was necessary, however poor it might be, and these N 70 V data are presented in Fig. 9C. The observations have been divided into six 4-hourly groups and the width of each block represents the mean catch per 250 m. haul. The number of observations at each depth and in each 4-hourly period are shown in Table 5. Before discussing this diagram it should be stressed that only the gross changes in vertical distribution can be considered. To emphasize this point cross-hatching has been used where, before correction for a 250 m. haul, the total for the particular time and depth is only one individual.

The gross daily changes in vertical distribution shown by this figure agree well enough with those seen in the N 100 B data. In addition it is evident that, for 16 out of the 24 hrs., a large proportion of the population is to be found between 750 and 250 m. There is, however, one anomaly. From 2000 hrs. to midnight the proportion of the population between 250 and 100 m. does not agree with that shown by the N 100 B; on the basis of Fig. 9C a peak would be expected between these hours in Fig. 9B. This may be partly due to the oblique nets sampling the water between 500 and 250 m., in which the population is reduced at this time.

Thus it appears that during the day the majority of the population of adolescent and adult *E. triacantha* is to be found between 500 and 250 m., part sinking below 500 m. for a short time around

midday, and that towards dusk there is a fairly rapid rise into the upper 250 m. of water, followed by a descent again in the early morning.

It seems probable, though by no means certain, that those animals which in daytime are between 500 and 750 m., do not migrate into the upper 100 m. during the night but remain within the 250–100 m. level, whereas those animals that spend the day between 500 and 250 m. probably enter the top 100 m.

There is no evidence from these data of the midnight sinking displayed by many other diurnal migrants. It may well occur, however, for it is unlikely to be detected with time intervals as widely spaced as these.

Various authors have shown that the extent of diurnal migration varies in some animals with their age, size and sex. Russell (1931) found that the smaller specimens of *Sagitta elegans* Verrill, 1873, rose to the surface before the larger ones at dusk and were later in leaving the surface at dawn; Southern

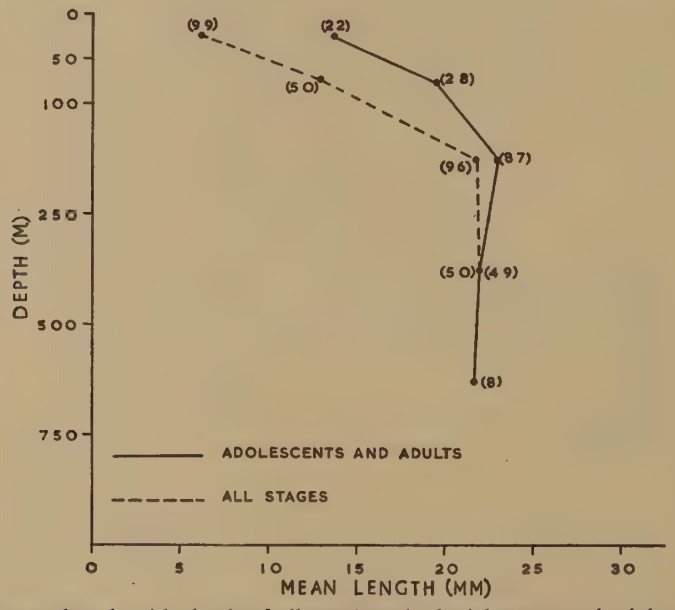

Fig. 10. Variation of the mean length with depth of all stages and of adolescents and adults only taken in the N70V between 2000 hrs. and midnight. The numbers of specimens upon which the means are based are shown in brackets.

and Gardiner (1932) showed that the reverse applied to *Daphnia longispina* O. F. Muller (1785) in Lough Derg. Motoda (1953), working at Lake Shikotsu in Japan, found that at midday the copepodites of *Acanthodiaptomus yumanacensis* (Brehm) were nearer to the surface than the adults. He also observed that the males of this species showed a greater sensitivity to light than the females. Cushing (1951) suggests that 'some animals become more sensitive to light as they grow older and others become less so'.

In Fig. 10 the mean lengths of adolescents and adults taken by the N70V between 2000 hrs. and midnight on the Greenwich meridian, have been plotted against depth. We are only concerned here with the relative lengths at different depths, the actual lengths are dependent upon the time of year the hauls were made. There is little doubt that there is a definite tendency for the smaller individuals to inhabit the upper 100 m. during this period whereas the larger ones are found below this level. It does not follow that the larger animals are never found in the upper layers, for specimens of over 35 mm. have frequently been taken in the 100–0 m. N100B at night; nor does it mean that the

smaller specimens are never found in deeper water. It would be interesting to compare the mean lengths at different depths between 0800 and midday but unfortunately the data are insufficient. There is an even more marked variation in the mean lengths when the larvae are included with these figures (pecked line) showing that there is a very strong tendency for them to inhabit the upper layers during the night. There is probably little or no significance in the reduction of mean length below 250 m. in this figure.

Although illumination is probably not the only factor involved in diurnal vertical migration, it is reasonable to assume that it plays the major part, and that any variation in length of daylight would influence the time spent at a particular depth. At 50° S there are approximately 8 hrs. more darkness

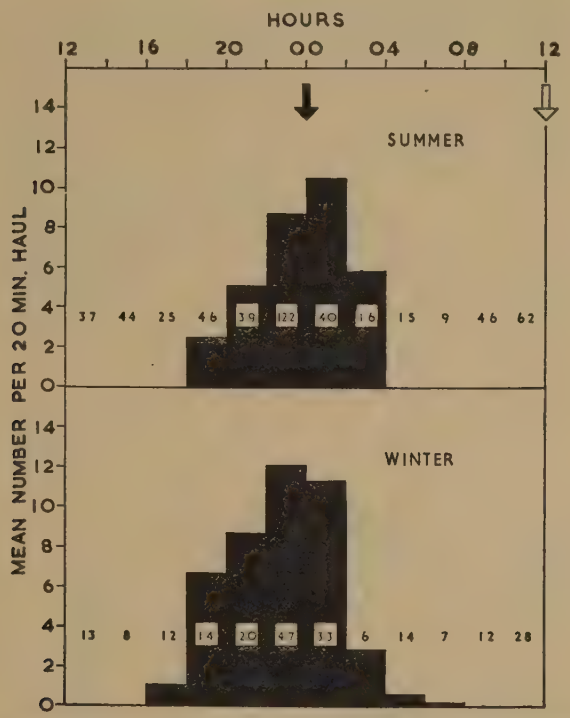

Fig. 11. The diurnal variation of the numbers of adolescent and adult *E. triacantha* in the upper 100 m. in winter and summer. The number of observations for each 2-hourly period are shown.

in winter than in summer, and it could be expected that this would affect the time spent in the upper 100 m. by *E. triacantha*. In Fig. 11 the mean numbers per 20 min. 100–0 m. N 100 B haul are plotted for summer and winter at 2-hourly intervals. As illumination is the primary consideration in this case summer has been taken as mid-September to mid-March and winter as mid-March to mid-September. This allows approximately three months either side of the longest and shortest days. From the figure there is not a great deal of difference in the time spent in the surface water by the majority of the animals, but the period during which no adolescent and adult *E. triacantha* are found in the surface at all is 6 hrs. shorter in winter than in summer. If there were sufficient data to compare winter and summer observations in the Bellingshausen Sea region it would probably be found that there was a greater difference, for the horizontal range of *E. triacantha* lies very much further south—between about 58° S and 69° S—where there is a difference of more than 13 hrs. between winter and summer darkness.

Most workers on plankton have at some time been faced by the problem of whether their results are affected by the organisms avoiding the net, in particular whether there is a greater degree of

avoidance during the day than during the night (Holt and Tattersall, 1905; Frost, 1932; Gardiner, 1934). Southern and Gardiner (1932) found that when they arranged a number of species in the order of the difference between day and night catches they were also in order of size. They concluded that the larger animals were more successful in avoiding the net and that this was a factor of some importance when considering the variation between day and night hauls. Hardy and Gunther (1935), when considering the vertical migration of the larvae of *E. frigida* Hansen, 1911, and *Thysanoessa* spp., found that there was no significant difference between the relative populations in the upper 1000 m. as shown by the nets by day and by night. The same seems to apply to adolescent and adult *E. triacantha*. In Table 6 the same data as were used in preparing Fig. 9C are given, except the mean catches for each depth range are based upon the actual catches and not those corrected for a 250 haul. The totals of these means can be taken as a measure of the total population, as shown by the N70V, in each 4-hourly period. Although these totals show a variation they do not indicate any significant increase in the amount of avoidance during the day. This does not mean that the animals do not avoid the N70V, it just shows that there is no appreciable diurnal variation in the amount of avoidance, and consequently reasonable comparisons can be made of day and night hauls. It should be pointed

Table 6. *The mean catch with the N70V in each depth range, uncorrected for a 250 m. haul and divided into 4-hourly periods. The totals represent the relative total population for each period. (These figures, corrected for a 250 m. haul have been used in preparing Fig. 9C. The numbers of hauls in each interval are given in Table 5)*

	Time (hr.)					
Depth (m.)	*12–16*	*16–20*	*20–00*	*00–04*	*04–08*	*08–12*
50–0	0·05	0·00	0·13	0·08	0·00	0·00
100–50	0·00	0·05	0·21	0·00	0·00	0·00
250–100	0·10	0·08	0·56	0·25	0·07	0·00
500–250	0·56	0·56	0·28	0·69	0·54	0·76
750–500	0·27	0·19	0·05	0·18	0·08	0·62
1000–750	0·08	0·06	0·00	0·09	0·00	0·00
Total	1·06	0·94	1·23	1·20	0·69	1·38

out that here we may be dealing with a special case and that this does not apply to all species. It has been shown above that the larger *E. triacantha*, i.e. those that would be more successful in avoiding the net, tend to inhabit deeper water where the increase in illumination during the day is not very great, and that in the upper waters, where the diurnal variation in illumination might be expected to have an effect, the animals are smaller and consequently less successful in avoiding the net. Mr Marr (personal communication) has found that in the case of adult *E. superba*, which inhabits the surface water and displays no diurnal migration, illumination has a very marked effect on the amount of avoidance, so much so that daylight hauls with the N70V very rarely take any adult *E. superba* at all.

Both Hardy and Gunther (1935) and Mackintosh (1937) have shown that the horizontal distribution of planktonic animals may be influenced by variations in their vertical distribution. Mackintosh suggested that populations, at least of certain common species in the Antarctic, could maintain their particular horizontal ranges by means of seasonal or diurnal vertical movements between water masses moving in different directions. To the south of the Antarctic convergence the directions of movement of the water masses are fairly well known (for details see Deacon, 1937). North of about 65° S the Antarctic surface water, a layer of cold water 100–250 m. in thickness, is moving to the east and north and below this lies the warm deep water which generally has a strong southerly component. We have seen above that the diurnal vertical movements of *E. triacantha* are sufficient for the animals to alternate between the two currents and it follows that, provided the relative speeds of the currents

are such that they counterbalance any difference in the times spent in each, the population would tend to be maintained in the same latitude. This does not imply, however, north and south movements in the same longitude, for the animals will always be moving towards the east during the night under the influence of the easterly component of the Antarctic surface water. The water movements to the north of the Antarctic convergence are not so well known as those to the south and it is difficult to say what effect vertical movements of animals might have on their horizontal distribution.

VERTICAL DISTRIBUTION OF LARVAE

The vertical distribution of the larval stages of *E. triacantha* has not been examined in great detail, since the material available is necessarily more limited than that for the adolescents and adults. This is partly due to the restricted breeding period and partly to the narrow latitudinal range of the larvae.

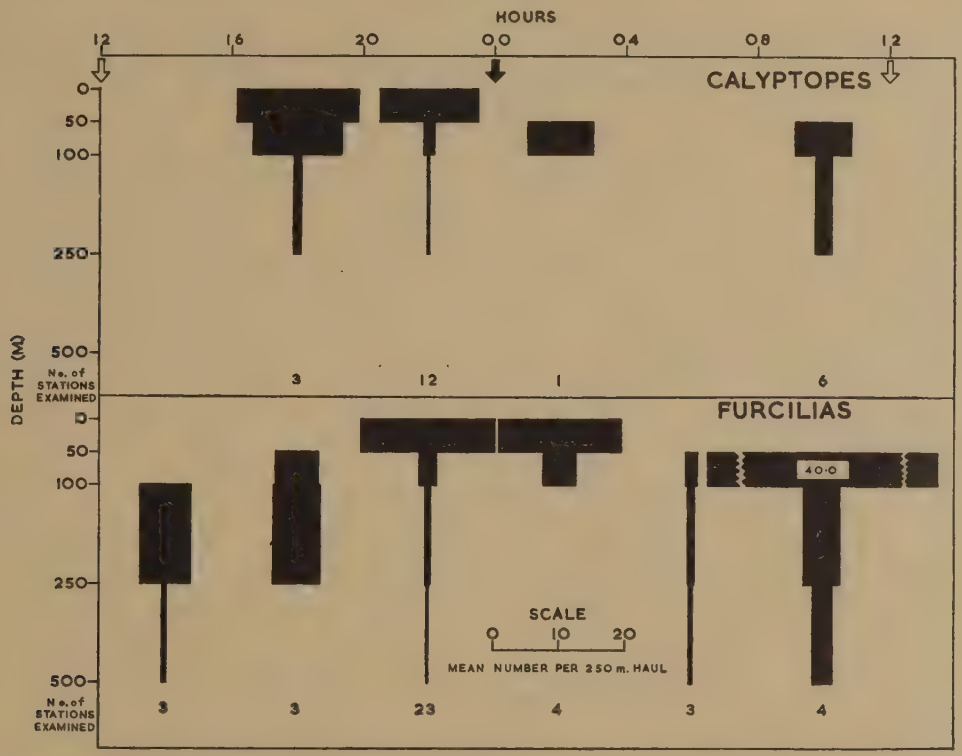

Fig. 12. The daily vertical distribution of calyptopes and furcilias from the N70V hauls. Only stations at which the larvae occurred have been used in calculating the mean number per 250 m. haul.

The data obtained from the material that has been examined are presented in Fig. 12. As in Fig. 9C the day has been divided in six 4-hourly periods and the mean catch per 250 m. haul calculated for each depth range in these periods. In calculating these means only stations at which calyptopes or furcilias occurred have been taken into account.

This figure suggests that, although the calyptopis stages probably perform a diurnal migration, it is confined mainly to the upper 100 m. The furcilias, however, show a more pronounced migration that extends between 250 m. and the surface. No calyptopes have been taken from below 250 m. and no furcilias from below 500 m. It has been mentioned above that some animals become sensitive to light with increasing age (Cushing, 1951) and the fact that the calyptopes do not descend below 250 m. during the day may be due to the lack of sensitivity to light or it may be due to a lack of

swimming power. Whatever the cause, there is little doubt that the depth attained during migrations increases with age.

To the south of the Antarctic convergence the larval stages are thus confined mainly to the north-easterly moving Antarctic surface water and the effect of this can be seen in their concentration in the region of the convergence.

SWARMING

There are no records of *E. triacantha* forming shoals on the same scale as *E. superba* (Mackintosh and Wheeler, 1929; Hardy and Gunther, 1935; Marr, 1956) or such as are sometimes seen in *Meganyctiphanes norvegica* (M. Sars), 1857 (Macdonald, 1927). On the contrary, the adults are generally rather sparsely but evenly distributed. Out of 292 night hauls between 100 m. and the surface with the N 100 B only ten contained more than fifty adolescents and adults. In nine of these the majority were juveniles in the post larval stage and in the tenth over 90% were under 20 mm. Thus, although swarming does not occur in the adults, occasionally hauls have been taken which contain numbers of the younger stages that are significantly larger than average. Two of these are of particular interest—at St. 1936 E, one of a series of stations repeated at approximately 3-hourly intervals, and at St. 2807. At St. 1936 E a flight of five 1 m. nets were towed horizontally at the following depths: 5, 22, 44, 86 and 133 m. The upper three nets contained 0, 517 and 8 larvae, respectively. These larvae must have been confined to a layer not more than 40 m. in thickness and very probably much less since the smaller number of larvae in the 44 m. net does not necessarily indicate a continuation of the concentration of larvae down to this level, since this net fished for a short time at 22 m. while the net above was being attached to the warp. It is not possible to determine the horizontal spread of this group of larvae owing to their diurnal vertical movements, but at St. 1936 D worked half a mile to the south two hours previously a similar flight of five nets fished at intervals down to 155 m. took a total of only forty-eight larvae.

At St. 2807 an N 100 B was fished from only 33 m. to the surface owing to bad weather, but even in this shallow haul 248 larvae were taken—a relatively dense swarm, at least for *E. triacantha*.

Marr (1956) finds that the older stages of *E. superba* accumulate in thin plate-like shoals and, although there is no evidence to show the horizontal extent of the patches of *E. triacantha* larvae that have been found, it seems probable that they too only occupy a comparatively narrow vertical range.

DEVELOPMENT AND GROWTH

Larval stages

The most comprehensive account of the larval stages of *Euphausia triacantha* is that by John (1936, p. 278). In this he describes and figures the second and third calyptopes and the seven furcilias. The first calyptopis is described by Rustad (1934, p. 19). Up to the present time no larval stage earlier than the first calyptopis has been found which can be referred with certainty to *E. triacantha*. Ruud (1932, p. 55) describes a metanauplius with a denticulate margin to the carapace which he suggests probably belongs to either *E. frigida* or *E. triacantha*; many metanauplii similar to this have been found in the 'Discovery' material, but as these have been taken not only within the range of *E. triacantha* but also to the north and south it seems certain that this type of metanauplius occurs in more than one of the southern species of *Euphausia*.

Table 7 shows the range and mean lengths of the ten larval stages examined; these data are plotted in Fig. 13. Measurements are from the anterior margin of the eyes to the tip of the telson. The mean length of the seventh furcilia is probably rather low, for there is tendency for the second pair of posterior-

lateral spines, the presence of which distinguishes this furcilia from the immediately post-larval forms, to break off in those furcilias which are shortly due to moult, and this results in their inclusion with the post-larvae. Although there is general agreement with John's results, the mean lengths of the fifth and sixth furcilias suggest that the latter stage may frequently be omitted. In the last four furcilia stages there is a gradual reduction in the number of terminal spines on the telson, from seven in the fourth furcilia to five in the fifth, three in the sixth and one in the seventh and all subsequent

Table 7. *Mean lengths and ranges of length of the larval stages from first calyptopis to seventh furcilia*

Stage	*No. measured*	*Range (mm.)*	*Mean length (mm.)*
C1	24	0·9–1·1	1·0
C2	27	1·6–2·3	1·9
C3	82	2·5–3·6	2·9
F1	110	3·4–4·8	4·4
F2	152	5·0–6·3	5·7
F3	171	6·0–7·4	6·9
F4	130	7·0–9·0	8·1
F5	73	8·0–10·5	9·6
F6	71	8·1–11·0	9·6
F7	59	8·2–11·3	10·0

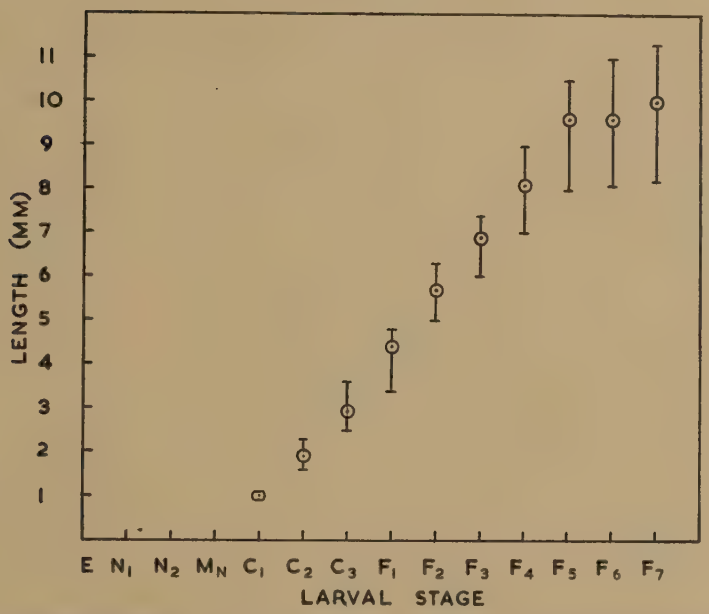

Fig. 13. The mean lengths (circles) and total range of length (vertical lines) of the larval stages from first calyptopis to seventh furcilia.

stages. In furcilias which are about to moult it is sometimes possible to see through the exoskeleton and to determine the number of terminal spines that will be present in the next stage (Lebour, 1926; Fraser, 1936; John, 1936). It has been possible to do this for a total of 141 fourth furcilias and 99 fifth furcilias. Table 8 shows the number and percentage of these fourth furcilias that were going to moult to fifth furcilias and the number and percentage that were going to moult directly to sixth furcilias omitting the five-spined stage. Similarly, the 99 fifth furcilias have been divided according to whether they were going to moult into sixth or directly into seventh furcilias. The percentages in Table 8 have been used in Fig. 14 to trace the developmental paths taken by one hundred fourth furcilias. Of the original hundred, nine moult to sixth furcilias and ninety-one to fifth furcilias by

the loss of four and two spines, respectively. Of these ninety-one fifth furcilias ten moult to sixth furcilias, whereas eighty-one miss out this three-spined stage and moult directly to the one-spined seventh furcilia. The nineteen sixth furcilias that have moulted from both fourth and fifth furcilias also moult to seventh furcilias. There are, then, three alternative routes from fourth to seventh furcilias, 4–5–6–7; 4–6–7; 4–5–7, and it is the last of these that the majority of larvae follow.

Table 8. *Variation in the number of terminal spines on the telson lost during ecdysis of the fourth and fifth furcilias*

Furcilia stage	*No. of terminal spines*	*No. of terminal spines in next stage*	*No. specimens examined*	%
4	7	5	129	91·4
4	7	3	12	8·6
		Total	141	100·0
5	5	3	11	11·1
5	5	1	88	88·9
		Total	99	100·0

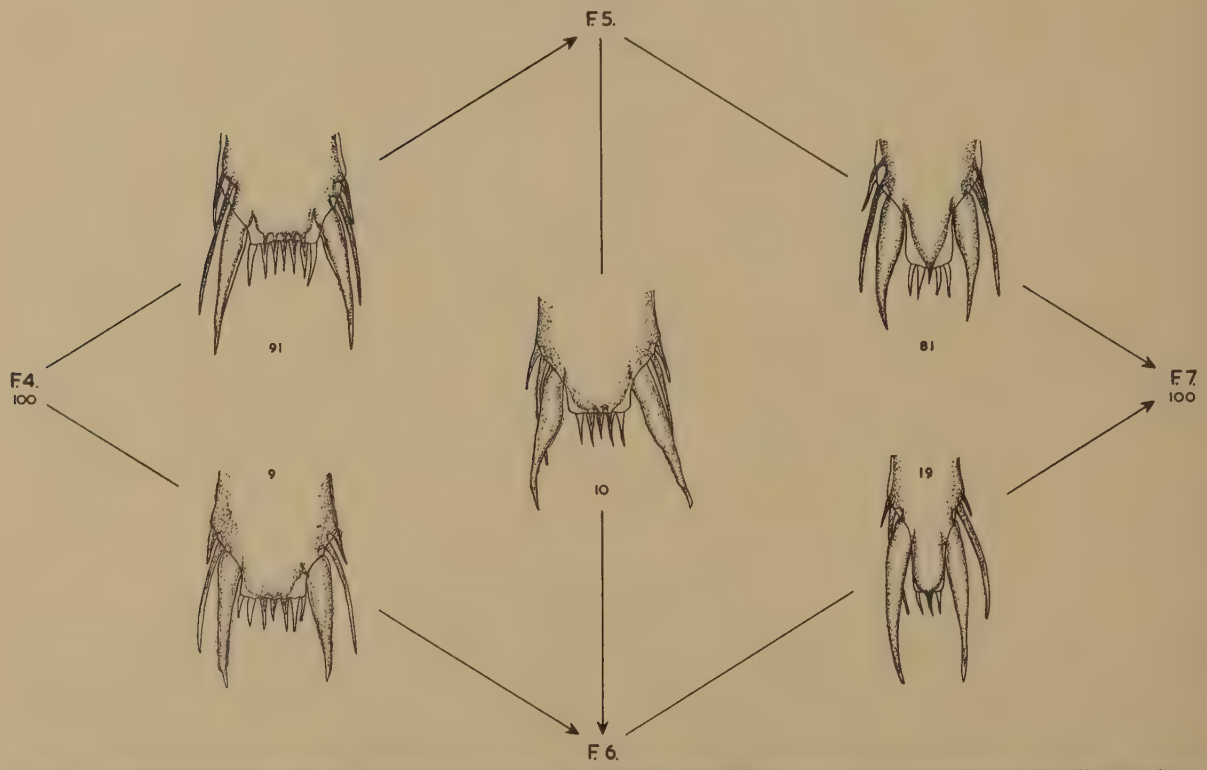

Fig. 14. The paths of development of one hundred fourth furcilias calculated from the percentages of fourth furcilias moulting to fifth or sixth furcilias and the percentages of fifth furcilias moulting to sixth or seventh furcilias (see Table 8). The figures show the arrangements of the spines on the telson in each stage and it can be seen how the number of terminal spines in the succeeding stage is determined.

Although it is now accepted that, within one species, larvae with certain combinations of setose and non-setose pleopods tend to be dominant and that the few other combinations that occur can be considered as variants, it is unusual for any of the furcilias which are recognized by the number of terminal spines on the telson, to be omitted. This point is emphasized by Boden (1955, p. 375) who,

writing of a furcilia of *Nematoscelis megalops* G. O. Sars, 1885, which bears one terminal spine, states 'I have called this the sixth furcilia, however, rather than the fifth. If it were the fifth the number of terminal spines would have to be reduced from five to one in one stage. This sequence has never been reported in any other life history and it seems justifiable to suspect that there is at least one stage with three terminal spines on the telson'. John (1936, p. 257) does record two larvae of *E. vallentini* in which seven spines are followed by three but this sequence does not occur in the majority of the larvae. Lebour (1926, p. 786), on the other hand, shows that this is the usual developmental sequence in *Nematoscelis microps* G. O. Sars, 1883 from the Mediterranean and it is confirmed by Gurney (1947, p. 60) from his Bermuda material.

In view of this and of the results obtained in the case of *E. triacantha* it is possible that when the larval development of more species is known it will be found that the omission of some of the later furcilia stages is more common than has previously been thought.

It is not intended to suggest that this necessarily applies in the case of *Nematoscelis megalops* but, as both Boden, who had, however, only a few late furcilia, and Frost (1935) failed to find larvae with three terminal spines, it is a point that will bear further consideration when more material is available.

Spawning

Both the time and the place of spawning can only be inferred from the presence of young larvae since neither eggs which can be identified as those of *E. triacantha*, nor gravid females have been found in the plankton. The earliest date at which first calyptopes have been found is 23 September and the latest 16 December. In order to obtain some indication of the time of spawning it is necessary to know the period required for development from the egg to the first calyptopis. The only estimate available is that from Lebour's (1924, p. 408) laboratory experiments on *Nyctiphanes couchii* (Bell), 1853, which gave a period of 8–9 days for development from nauplii free in the egg-sacs to the first calyptopes. If the assumption is made that a similar period is required in *E. triacantha*, spawning could be expected to occur from mid-September to early December, although it must occasionally take place later than this, for a few third calyptopes (a total of eighteen from five stations) have been taken in January and early February. However, the maximum number of calyptopes are found in late October and November and the main spawning almost certainly takes place during these months.

It is probably reasonable to assume that spawning takes place in the region of maximum abundance of larvae, that is in a belt 200 miles wide south of the Antarctic convergence. There is, however, no evidence regarding the depth at which it occurs.

Adolescents and adults

Prior to the development of the external reproductive organs, the petasma in the male and the thelycum in the female, the only external character distinguishing the sexes in *E. triacantha* is the presence of setae on the coxopodite of the sixth thoracic limb of the male and their absence in the female. Thus *E. triacantha* differs from *E. superba* in which the male has a narrower and more shallow carapace than the female and in which there are also differences in the shape of the rostrum and of the spine at the anterior lateral corner of the carapace (Bargmann, 1937, p. 328). However, the sex of nearly all post-larval *E. triacantha* can be determined by examination of the reproductive system.

The development of the reproductive systems follows very closely the patterns described by Bargmann (1937) for *E. superba* and it is not proposed to describe it in detail here. In the male the only differences appear to be the number of lobes of the testis—twelve in *E. triacantha* as compared with fifteen in *E. superba*—and, in *E. triacantha*, the lesser degree of coiling of the vasa deferentia between the anterior and posterior flexures.

In the immediately post-larval female the ovary is unlobed and saddle-shaped. Growth takes place steadily, the ovary becoming lobed and extending ventrally on to the thoracic muscles and posteriorly into the abdominal region. Development of the thelycum takes place simultaneously with the growth of the ovary and by the time the thelycum reaches the adult shape and is heavily chitinized the ovary is usually touching or overlapping the thoracic muscles and the shell gland is just starting to develop.

Eggs were measured under a low power binocular microscope in 108 *E. triacantha* at various stages of maturity, the smallest female in which this was possible being 20 mm. in length and in which the eggs were 0·05 mm. in diameter. The smallest female *E. superba* in which Bargmann (1945, p. 115) found eggs of this size was 27 mm. When they can first be measured all the eggs on the dorsal surface of the ovary are of uniform size, but as the ovary matures the eggs in the region of the oviduct increase in size more rapidly than the others and it is in this region that the largest eggs are always found. At a slightly later stage the eggs near the tips of the lobes enlarge and a graded series is formed from the median part of the ovary where the eggs are small to the outer edges of the lobes where they are large. However, even in the most mature female examined, in which the largest eggs measured 0·44 mm. and were opaque and yolky in appearance, there still remained a narrow border of small eggs (0·05 mm. diameter) round each of the lobes, and it is probable that these eggs never develop any further. Only two females have been taken which give the appearance of having spawned. However, in one of these the thelycum contained two full spermatophores and in the other, one full and one damaged spermatophore. In both these the ovary had the original saddle-shape described by Bargmann (1937, p. 348) for spawned *E. superba* and the oviducts could be seen as wide flat bands whereas in the young stages with this type of ovary they are narrow.

Out of eighty-five female *E. triacantha* carrying spermatophores fifty-three were full, ten half-full and fourteen empty. The remaining eight carried one full spermatophore, the other having been broken off, and these can probably be included with those with full spermatophores. Although these numbers are small this suggests that the sperm-mass remains in the spermatophore for some considerable time before migrating into the thelycum. It is interesting to compare this with Bargmann's observation (1945, p. 117) that 'of 556 females (*E. superba*) carrying spermatophores, only 102 were full, showing that the migration of the sperm-mass into the thelycum must be a rapid process'.

Growth rate

The life cycle of *E. triacantha* takes two years to complete as in *E. superba* (Ruud, 1932; Bargmann, 1945). This is shown in Fig. 15 in which the data from hauls down to 500 m. with the N 100 B and N 70 V have been used to plot the length frequencies for each month of the year. The animals have been divided into two-millimetre groups and the number in each group expressed as a percentage of the total number measured in each month. These totals are shown at the top of the figure. In calculating the larval frequencies measurements have not been made; instead it has been considered sufficient to use the mean length for each stage shown in Fig. 13 (p. 331). In view of the fact that the data have been taken from many different localities in different years the results presented in Fig. 15 are remarkably consistent, and this suggests that there is little variation in the rate of growth from region to region and from year to year.

In September three distinct size groups can be seen: the larvae, which result from a recent spawning, the adolescents, which were spawned in the previous year, and the adults, spawned two years previously and now due to spawn themselves. The larvae in September consist entirely of first calyptopes. In the succeeding months the young stock is gradually built up, the predominant stages being first and second furcilia in November (about 4–6 mm.), second and third furcilia in December and fourth to seventh furcilia in January and February. By April nearly all the 0-year group have become

post larval. From December onwards there are, in Fig. 15, still slight indications of three size groups and it is possible that a small part of the population does not spawn in the third spring but lives to spawn in the spring of the fourth year. The males of over 30 mm. in December carry ripe spermatophores, and in the next two months an increasing number of undoubted 1-year group males attain sexual maturity until, by March, practically all those over 25 mm. have reached the mature condition. On the other hand, during these months all females, including those over 30 mm. in length, have immature ovaries. Thus it is not possible to be certain whether these larger size groups are made up of animals that have grown more rapidly and the males have become sexually mature rather early, or whether they represent a small part of the population having a three-year cycle.

Considering only those males which clearly belong to either the 0-year group or 1-year group the time taken to reach various degrees of maturity can be determined. The period of adolescence, that is the period during which the reproductive system is still developing (Bargmann's stages 1–5), lasts

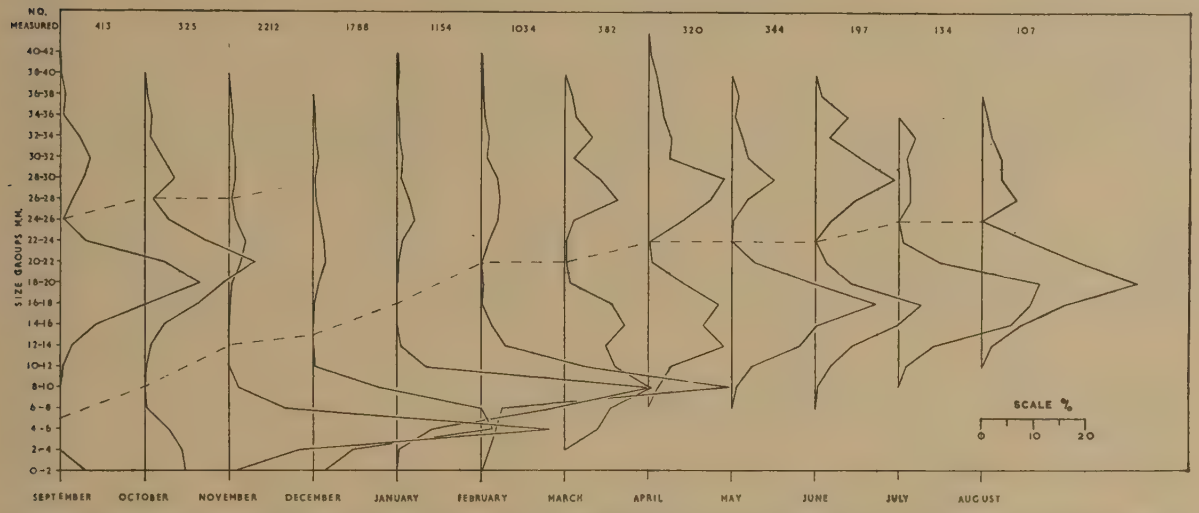

Fig. 15. Monthly percentage length frequencies of *E. triacantha*. The number of specimens measured in each month is shown at the top. The pecked lines divide the population into year groups. These groups have been used in preparing the growth curve, Fig. 16.

from April to about the following November. During this and the next month an increasing number of males are found with imperfect spermatophores in the spermatophore sacs or ejaculatory ducts, and, using Bargmann's criteria, these can be considered as having entered the adult phase. During January and February a large proportion are found with mature spermatophores in both the spermatophore sacs and the ejaculatory ducts, and by March nearly all have reached this fully adult condition and are presumably ready for pairing. It seems probable, however, that pairing is generally delayed, because, although from January onwards a few females are found carrying spermatophores, it is not until June that the majority do so.

A complete analysis of egg sizes has not been made, but it is apparent from those that have been measured that eggs of over 0·3 mm. in diameter begin to appear in the ovaries about May, and that the number of females with such eggs and the number of eggs of this size present in each ovary increases until, in August very nearly all the adult females have ovaries with at least some large eggs. The two females, mentioned above, with the appearance of having spawned, were taken in late September.

The growth rate during the two years of the life cycle can best be seen by separating the year groups

and calculating the mean length for each month. The 0- and 1-year groups are readily distinguished and the points at which they have been separated are indicated in Fig. 15 by the lower pecked line.

The 1- and 2-year groups can also be separated in September, October and November as all the males above the upper pecked line have fully developed spermatophores and nearly all the females have well-developed ovaries with large eggs scattered about the surface, whereas these characters are

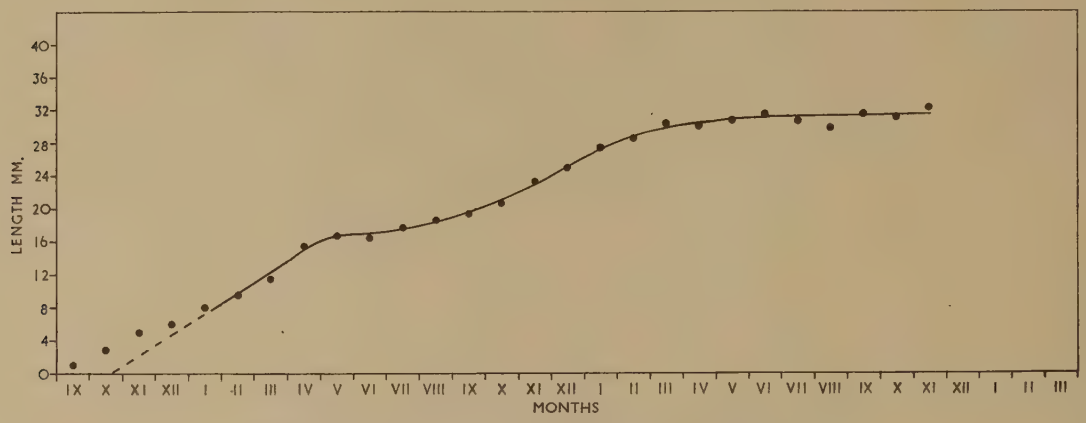

Fig. 16. Growth curve for *E. triacantha* taken from Fig. 15.

Table 9. *Mean monthly lengths of* Euphausia triacantha

Months	*Mean length (mm.)*	*No. of obs.*	*Mean length (mm.)*	*No. of obs.*	*Mean length (mm.)*	*No. of obs.*
September	1·0	20	19·3	319	31·5	74
October	2·8	64	20·6	221	31·1	40
November	5·0	1954	23·2	176	32·2	82
December	6·0	1620	24·9	168	—	—
January	8·1	1052	27·5	105	—	—
February	9·6	880	28·5	154	—	—
March	11·5	270	30·2	112	—	—
April	15·5	166	30·0	154	—	—
May	16·7	281	30·7	63	—	—
June	16·4	110	31·4	87	—	—
July	17·7	122	30·7	12	—	—
August	18·5	89	29·8	18	—	—

absent in the smaller size groups. For the purposes of calculating the mean monthly lengths for Fig. 16 it has been assumed that after the end of November all those animals in size groups above the pecked line in Fig. 15 belong to the 1-year group. The mean lengths and the number of observations on which they are based are shown in Table 9. The mean lengths for September to December do not take account of larvae not yet hatched and the estimated curve for these months is shown in Fig. 16 as a pecked line which starts at the estimated mean time of hatching (see p. 333) and joins the rest of the curve in January when no more larvae are being hatched.

During the first six and a half months after hatching, that is from mid-October to the end of April, *E. triacantha* grows fairly steadily at a rate of about 2.5 mm. per month. With the onset of winter the rate of growth slows down to less than half this, the curve giving an average of 1 mm. per month for May to August. From September to February of the second year the rate is again increased though

it does not reach that of the first summer, the average being 1·7 mm. per month, and after March little or no further growth takes place. The two periods of rapid growth during the life cycle correspond with the periods of phytoplankton abundance described by Hart (1942) for his 'Northern Region'.

A comparison of this growth curve with Bargmann's curve for *E. superba* (1945, p. 129), shows that, whereas *E. triacantha* stops growing in the first half of the second year of life, *E. superba* is still growing during the early part of the third year. Thus it appears that the larger size of *E. superba* is reached by a longer period of growth rather than by a faster average rate.

SUMMARY

1. The material upon which this paper is based was contained in samples taken during oblique hauls with the 1 m. net and vertical hauls with the 70 cm. closing net.

2. The horizontal range of the adolescents and adults extends from Subantarctic water southwards to the northern limits of the East Wind and Weddell drifts. The region of maximum abundance is a circumpolar belt extending from 150 miles north to 200 miles south of the Antarctic convergence and there is little or no seasonal variation in this distribution. The extreme range of surface temperature is −1·80–11·88° C., the greater part of the population living between 2 and 8° C. for most of the year.

3. The distribution of *E. triacantha* is compared with that of *E. superba*, and it is shown that the southern limit of the former roughly coincides with the northern limit of the latter.

4. The region of maximum abundance of larvae is a belt extending for 200 miles south of the Antarctic convergence.

5. All stages from first calyptopis upwards perform a diurnal migration which becomes more marked with increasing age. The lower limit of the vertical range does not normally extend below 750 m.

6. Adolescent and adult *E. triacantha* do not form swarms and indeed are rather evenly distributed, but there is evidence of occasional small-scale swarming in the larvae.

7. The mean lengths of the larval stages have been calculated and it is shown that the furcilia stage with three terminal spines on the telson is usually omitted.

8. Spawning takes place mainly in October and November and it is presumed to occur in the region of maximum abundance of larvae.

9. The development of both the male and female reproductive systems is similar to that of *E. superba*.

10. Monthly length frequencies show distinct year groups. The normal life cycle takes two years from hatching to breeding. Growth is slower in winter than in summer and ceases earlier than in *E. superba*.

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